

## Two new species of Australian *Eutarsopolipus* (Acariformes: Podapolipidae) from *Nurus medius* (Coleoptera: Carabidae)

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### Abstract

*Eutarsopolipus burwelli* **sp. nov.** and *E. echinatus* **sp. nov.** (Acariformes: Podapolipidae) are described from *Nurus medius* Darlington, 1961 (Coleoptera: Carabidae), a large burrowing carabid beetle found in the rainforests of coastal central Queensland, Australia. *Eutarsopolipus burwelli* belongs to the *ochoi* species group, which is herein refined, and *E. echinatus* is placed tentatively in the *pterostichi* species group. A revised key to the species groups of *Eutarsopolipus* is provided. The synhospitalic species of *Eutarsopolipus* are reviewed and synhospitality within the genus is discussed.

**Key words:** Heterostigmatina, key, insect parasites, species groups, synhospitality, taxonomy

### Introduction

*Eutarsopolipus* Berlese, 1913 (Acariformes: Podapolipidae) is the largest genus of Podapolipidae with 71 described species (Katlav & Hajiqanbar 2018), all of which are subelytral parasites of carabid beetles. Regenfuss (1968) separated the genus into several species groups, subsequently augmented by other authors, with up to 14 species groups now recognised (Husband & Husband 2009). This informal classification aids identification and provides a useful means of discussing purported relatedness between species, but a phylogenetic test of these species groups has not yet been accomplished.

The genus is widespread, being found on every continent where carabids exist. In Australia, just five species are described: *Eutarsopolipus megacheli* Husband and Macfarlane, 1999 and *E. secundus* Husband and Macfarlane, 1999, both from *Catadromus lacordairei* Boisduval; and *Eutarsopolipus earnshawi* Constantine and Seeman, 2014, *E. lambkinae* Constantine and Seeman, 2014 and *E. rutherfordae* Constantine and Seeman, 2014, from *Cratoferronia phylarchus* (Sloane), *Notonomus angustibasis* Sloane and *Trichosternus subvirens* (Chaudoir), respectively. All of these beetles are members of the Pterostichinae, hinting at a rich diversity of podapolipid mites on this diverse subfamily of beetles.

The biology of *Eutarsopolipus* has not been studied, but like other beetle-associated species of Podapolipidae, sexual transmission is thought to be their primary—or only—means of transfer between hosts (e.g., Hurst *et al.* 1995; Seeman & Nahrung 2004). This means of transmission is probably a major factor for their apparent high host specificity, with many species being recorded from one host beetle or just a few closely related species (e.g., Eidelberg 1994; Hajiqanbar & Mortazavi 2012; Mortazavi *et al.* 2014).

Herein, I describe two new species of *Eutarsopolipus*, each from different species groups, from the pterostichine carabid species *Nurus medius* Darlington. This beetle species is a large, burrowing carabid found in the subtropical rainforests of Eungella National Park, located on the central coast of Queensland.

### Materials and methods

Mites were collected from beetles preserved in 75% ethanol or from pinned beetles in the collection of the Queensland Museum. Pinned beetles were soaked in hot water for at least 15 minutes before their elytra were lifted and the

subelytral space jetted with ethanol to dislodge mites. Each mite specimen was mounted, examined and measured following the method described by Seeman and Nahrung (2005). Plate lengths were taken at their midpoints; plate widths are not given for plates wrapped around the body; distance between setae represents the distance from setal insertion to setal insertion; vestigial "setae" are represented by the acetabulum only, minute setae do not extend past the acetabulum. The tiny tarsal setae *p'* and *u''* are given in setal counts and the description. Sometimes these setae are not included because they are difficult to observe, but here *u''* is always apparent and *p'* was often apparent, so they are included. Morphological terminology follows Lindquist (1986).

Drawings were prepared with the aid of a camera lucida on a Nikon Eclipse 80i microscope. All measurements are given in micrometres. The measurement of the holotype is given first, where relevant, followed by the range of all specimens. Abbreviations: ANIC (Australian National Insect Collection, Canberra); ANZSES (Australia and New Zealand Scientific Exploration Society); HR# (Host registration number); IN (Entomology Site Code); NP (National Park); QM (Queensland Museum); SC (Sample Code); SF (State Forest); ZMH (Zoological Museum Hamburg).

## Results

### Family Podapolipidae Ewing, 1922

#### Genus *Eutarsopolipus* Berlese, 1913

*Type species: Tarsopolipus lagenaeformis* Berlese, 1911, by original designation.

**Diagnosis.** *Female.* Three pairs of well-developed legs. Prodorsal plate present, plates C, D, EF usually present, sometimes divided, rarely absent, plate H usually greatly reduced or absent; setae *vl*, *sc1*, *sc2*, *c1*, *c2*, *d*, *f* present, setae *e* absent, setae *h* present or absent. Pseudolegs usually absent. Respiratory system present or absent. Gnathosoma ovoid, with two pairs of setae. Pretarsi I–III with well-developed ambulacrum, claws present or absent. Tibia II–III without spine-like setae. *Male.* Three pairs of legs. Genital capsule terminal, elongate or trapezoidal. Prodorsal setae developed to vestigial. Plate C–D–EF with three pairs of setae. Ventral idiosomal setae present. Pretarsi I–III with well-developed ambulacrum, claws present or absent. Femora I–III setation (0–3)–0–0, genua I–III setation (0–2)–(0–1)–(0–1), tibia I with or without seta *k*. *Larva:* Plate EF present; plate D sometimes in deep concavity of plate C; plate H present or absent, not on terminal capsule-like segment; ventral idiosomal setae present; pretarsi I–III with well-developed ambulacra, claws present or absent. Larval male: absent. Migrating life stage: probably larva. Host insect family: Carabidae.

#### *Eutarsopolipus burwelli* sp. nov.

**Diagnosis.** All life stages: respiratory system absent; tarsus II without solenidion; femur I with three setae; genu I with two small, spine-like setae (*l'*, *l''* present), genua II–III with one seta (*l'* present); claws present on legs I–III. Adult female: gnathosomal length 66–70, width 62–67, cheliceral stylets long, 75–95; idiosomal setae *d* 10–14, *f* 8–13, *h* 5–6; femur I seta *l'* 2–4; genu I setae 2–3; tarsi II–III with seta *pv'* absent. Larviform adult male: dorsal setae *vl*, *sc1*, *sc2*, *c1*, *c2*, *d*, *f* developed; leg setation same as female. Larval female: plates C and D separate; seta *h2* short, 11–13.

**Type material.** 18 females, 5 males, 15 larvae, all ex *Nurus medius*, as follows. **Australia: Queensland.** Holotype female, Eungella NP, Mt William, Site 1, 1234 masl, 21.016°S 148.598°E, 14 Nov. 2013, SC 25844, C. Burwell (QMS 110124). Paratypes: **6 females, 3 larvae**, same data as holotype (QMS 110125–33); **1 female, 1 male**, Crediton SF, 28°18'28"S 148°32'33"E, 1 Dec–31 Dec 1993, IN9787, ANZSES, HR# T110024 (QMS 110134–35); **7 females, 9 larvae**, Eungella NP, Dalrymple Heights, 21° 8'12"S 148°29'30"E, IN7864, 6 Jan. 1973, J. Hammond, HR# T82062 (QMS 110136–45; 1 female ZMH-A0002396, 1 larva ZMH-A0002398; 1 female ANIC 52-003930, 1 larva ANIC 52-003931); **2 females, 1 male**, Eungella NP, Upper Cattle Creek, 21°1'41"S 148°36'11"E, 17 Nov. 1992, IN6186, G. Monteith, G. Thomson, H. Janetzki, HR# T82055 (QMS 110146–48); **1 female, 1 larva**, Mount William, 21° 1' 5"S 148°35'57"E, 21 Dec. 1992–10 Jan. 1993, IN5952, ANZSES, HR# T82066 (QMS 110149–50);

**3 males, 1 larva**, Mt Macartney, 20°49'57"S 148°33'7"E, 19 Nov. 1992–15 Apr. 1993, IN5936, HR# T82039 (QMS 110151-52; 1 male ANIC 52-003932; 1 male ZMH-A0002397).

*Type deposition.* Holotype and most paratypes deposited in QM. One female, one male, one larva deposited in ANIC, one female, one male, one larva deposited in ZMH.

**Description. Female** (Figs 1–3, *n* = 18). *Gnathosoma*. Length 70 (66–70), width 67 (62–67). Palp length 16 (15–16). Cheliceral stylets 90 (75–95), pharynx width 21 (15–21), dorsal gnathosomal setae (*ch*) 36 (30–37), ventral setae (*su*) 18 (15–18), distance between ventral setae (*su-su*) 21 (18–23).

*Idiosoma*. Moderately physogastric, ovate. Length 325 (310–450), width 290 (270–370). Respiratory system absent. Prodorsal plate length 88 (83–99), with setae *v1* 13 (9–13), *v2* vestigial, *sc1* 14 (12–15), *sc2* 95 (95–120); *v2* anteromesad *sc1*. Distance between setae *v1-v1* 57 (52–58), *sc1-sc1* 108 (105–110), *v1-sc1* 33 (28–34), *v2-v2* 68 (65–69), *sc2-sc2* 155 (125–155), *sc1-sc2* 42 (35–44). Plate C length 67 (63–70), setae *c1* 15 (15–17), setae *c2* 15 (11–16), distance between setae *c1-c1* 105 (88–110), *c1-c2* 88 (78–93); often with pair of pore-like structures laterad setae *c1*. Plate D length 64 (57–64), setae *d* 13 (10–14), *d-d* 165 (160–180), cupuli *ia* antieriad to anterolaterad setae *d*. Plate EF length 65 (60–65), setae *f* 13 (8–13), *f-f* 145 (130–145); cupuli *im* antieriad to anterolaterad setae *f*. Plate H length 30 (17–30), width 94 (94–115), setae *h* 5 (5–6). Venter: coxal setae short, usually simple (anomalous star-like form in holotype specimen), *1a* 3 (2–3), *2a* 5 (4–6), *3a* 7 (6–7), *3b* 6 (6–8). Alveoli *1b*, *2b* apparent. Distance between setae *1a-1a* 40 (40–48), *2a-2a* 58 (58–66).

*Legs*. Setal counts legs I–III, femur-tarsus: 3-2-6(+ $\phi$ )-9(+ $\omega$ ), 0-1-4-7, 0-1-4-7. Leg I: femur I, *d* minute, *l'* 4 (2–4), *v''* 17 (13–17); genu I, *l'* 3 (2–3), *l''* 3 (2–3); tibia I, *d* 82 (70–82), *l'* 6 (5–8), *l''* 11 (8–11), *k* 6 (4–6), *v'* 8 (5–8), *v''* 10 (10–14),  $\phi$  10 (10); tarsus I, *tc'* 17 (14–17), *tc''* 16 (15–17), *pl'* 9 (8–11), *pl''* 16 (16–20), *pv'* 3 (3), *pv''* 3 (4), *s* 7 (6–7),  $\omega$  3 (3), *p'* 2 (2), *u''* 1 (1–2). Leg II: genu II, *l'* 4 (3–4); tibia II, *d* 60 (50–60), *l'* 8 (7–8), *v'* 14 (12–15), *v''* 25 (23–29); tarsus II, *tc'* 6 (5–6), *tc''* 65 (55–65), *pl'* 3 (3), *pv''* 3 (3–4), *u'* 8 (7–8), *u''* 1 (1–2), *p'* 1 (1). Leg III: genu III, *l'* 3 (3–4); tibia III, *d* 47 (45–50), *l'* 7 (7–10), *v'* 15 (10–15), *v''* 21 (17–26); tarsus III, *tc'* 6 (5–6), *tc''* 60 (50–60), *pl'* 3 (3–4), *pv''* 3 (3–4), *u'* 8 (7–8), *u''* 1 (1), *p'* 1 (1). Genu I, *l'-l''* blunt, peg-like; tarsus I *s* spine-like. Tarsi II–III *u'* spine-like, bifid, *tc'*, *pv'*, *pv''* spine-like. Claws on legs I–III (1-2-2) well developed.

**Larviform adult male** (Fig. 4; *n* = 5; square brackets indicate two male specimens with different measurements)

*Gnathosoma*. Length 30–33 [37–38], width 29–32 [34–35]. Palp length 10–14. Cheliceral stylets 22–26, pharynx width 6–9, *ch* 8–11 [13], *su* 6–9, *su-su* 13–14.

*Idiosoma*. Length 150–175, width 120–145. Prodorsal plate length 52–57 [59–63], width 86–97 [110–115], with setae *v1* 5–7, *v2* vestigial, *sc1* 4–6, *sc2* 65–80; *v2* anteromesad *sc1*. Distance between setae *v1-v1* 22–26 [27–29], *sc1-sc1* 45–49 [52–57], *v1-sc1* 15–19 [20–21], *v2-v2* 26–29 [30–34], *sc2-sc2* 53–63 [67], *sc1-sc2* 20–22 [25–28]. Plate CD length 45–50 [58–65], width 105–115 [140–145], setae *c1* 4–7, *c2* 5–9, *d* 4–7; distance between setae *c1-c1* 38–45 [51–56], *c1-c2* 28–33 [38–40], *d-d* 33–36 [44]; cupuli *ia* anterolaterad setae *d*. Plate EF bowed, posterior margin concave, length 24–28, width 40–43 [55–56], setae *f* 2–4, distance *f-f* 23–27 [35–37]; cupuli *im* anterolaterad setae *f*. Genital capsule length 18–26, width 27–28 [33–37], setae *h* minute. Venter: coxal setae *1a* 2–3, *2a* 3–4, *3a* 3–5, *3b* 4–5, alveoli *1b*, *2b* apparent. Distance between setae *1a-1a* 21–24, *2a-2a* 23–25 [28–36].

*Legs*. Setal counts legs I–III same as female; setal form similar. Leg I: femur I, *d* minute, *l'* 2, *v''* 5–6; genu I, *l'*, *l''* 1–2; tibia I, *d* 40–45, *l'* 2 [3–4], *l''* 3–4, *v'* 2–3, *v''* 7–9,  $\phi$  7 [9–10], *k* 2–3; tarsus I, *tc'* 12–14, *tc''* 13–14, *pl'* 5–7, *pl''* 13–14, *pv'* 1–2, *pv''* 1–2, *s* 4, *p'* 1, *u''* 1,  $\omega$  2. Leg II: genu II, *l'* 2–3; tibia II, *d* 25–27, *l'* 5–8, *v'* 10–14, *v''* 15–17; tarsus II, *tc'* 3–5, *tc''* 24–26, *pl'* 2–3, *pv''* 1–3, *u'* 4–5, *u''* 1. Leg III: genu III, *l'* 2; tibia III, *d* 18–20, *l'* 5–6, *v'* 8–11, *v''* 14–15; tarsus III, *tc'* 3–4, *tc''* 25–27, *pl'* 2–3, *pv''* 2–3, *u'* 4–6, *u''* 1.

**Larval female** (Fig. 5; *n* = 15). *Gnathosoma*. Length 55–61, width 52–56. Palp length 15–16. Cheliceral stylets 65–80, pharynx width 12–15, *ch* 30–38, *su* 8–12, *su-su* 15–20.

*Idiosoma*. Length 225–280, width 170–245. Prodorsal plate length 76–87, width 135–160, with setae *v1* 8–11, *v2* vestigial, *sc1* 7–10, *sc2* 130–140; *v2* anterolaterad *sc1*. Distance between setae *v1-v1* 35–40, *sc1-sc1* 72–78, *v1-sc1* 23–27, *v2-v2* 44–47, *sc2-sc2* 86–98, *sc1-sc2* 35–45. Plate C length 57–58, setae *c1* 12–17, setae *c2* 8–12; often with pair of pore-like structures laterad setae *c1*. Plate D length 48–50, width 105–120, setae *d* 8–11, distance between setae *c1-c1* 56–68, *c1-c2* 47–57, *d-d* 67–77; cupuli *ia* anterolateral setae *d*, distance *ia-d* 2–4. Plate EF length 40–47, width 85–100, setae *f* 9–11, distance *f-f* 54–61; cupuli *im* antieriad setae *f*, distance *im-f* 4–5. Plate H length 29–36, width 21–23, seta *h1* long, ca. 180, seta *h2* short, 11–13. Venter: coxal setae all short, *1a* 3–4, *2a* 4–5, *3a* 4–6, *3b* 6–7. Distance between setae *1a-1a* 28–31, *2a-2a* 35–39.



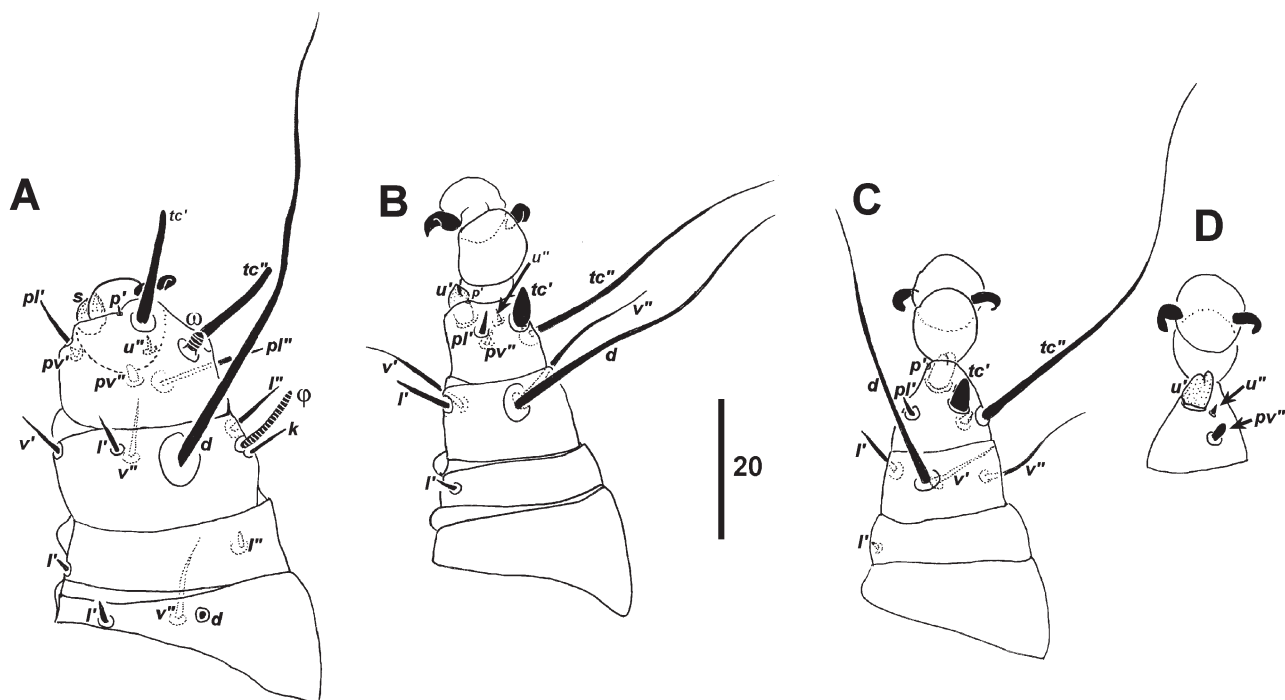
FIGURE 1. *Eutarsopolipus burwelli* sp. nov., adult female, dorsum.

*Legs.* Setal counts legs I–III same as adult female; setal form similar. Leg I: femur I, *d* minute, *l'* 2–3, *v''* 10–12; genu I, *l'* 2, *l''* 2–3; tibia I, *d* 75–85, *l'* 11–13, *l''* 12–15, *v'* 4–5, *v''* 12–15,  $\phi$  10–12, *k* 4–5; tarsus I, *tc'* 15–17, *tc''* 15–18, *pl'* 7–8, *pl''* 19–24, *pv'* 1–2, *pv''* 1–2, *s* 5–6, *p'* minute, *u''* 1–2,  $\omega$  2–3. Leg II: genu II, *l'* 1–3; tibia II, *d* 40–45, *l'* 8–9, *v'* 14–15, *v''* 19–21; tarsus II, *tc'* 3–5, *tc''* 25–36, *pl'* 2–4, *pv''* 2–3, *u'* 5–6, *u''* 1. Leg III: genu III, *l'* 2–3; tibia III, *d* 45–50, *l'* 7–8, *v'* 15–17, *v''* 16–20; tarsus III, *tc'* 3–5, *tc''* 25–35, *pl'* 2–4, *pv''* 1–2, *u'* 5–6, *u''* minute–1.



**FIGURE 2.** *Eutarsopolipus burwelli* sp. nov., adult female: (A) venter; (B) setae *1a*, holotype specimen (anomalous form), detail; (C) setae *1a*, paratype specimen (typical form), detail.





**FIGURE 3.** *Eutarsopolipus burwelli* sp. nov., adult female: (A) leg I, dorsal view; (B) leg II, dorsal view; (C) leg III, dorsal view; (D) tarsus III, ventral view.

**Etymology.** It is with pleasure that I name this species for my colleague Dr Chris Burwell, the collector of several host beetles for Australian mites, including this species.

**Differential diagnosis.** *Eutarsopolipus burwelli* is a member of the *ochoai* species group (Husband 1995; Constantine and Seeman 2005). Within this group, this species is very similar to *E. rutherfordae* in having females with a reduced plate H, females and males lacking setae *pv'* and tiny, spine-like genual setae *l'* and *l''*. Females and larvae of each species are easily distinguished, but males and larvae are almost identical. Females are most easily separated by the size of the gnathosoma (66–70 × 62–67 in *E. burwelli* versus 53 × 53 in *E. rutherfordae*), cheliceral stylets (75–95 in *E. burwelli* versus 60 in *E. rutherfordae*), size of setae *d* and *f* (8–14 in *E. burwelli* versus 22–25 in *E. rutherfordae*), and the size of tibia I seta *l'* (5–8 in *E. burwelli* versus 13 in *E. rutherfordae*). The larger gnathosoma of *E. burwelli* also presents in the larva (55–61 × 52–56 in *E. burwelli* versus 47 × 47 in *E. rutherfordae*), as do the longer cheliceral stylets (65–80 in *E. burwelli* versus 48 in *E. rutherfordae*).

**Remarks.** Two males had several measurements somewhat larger than the other specimens. Although these seem different, size variation in male podapolipid mites is a known phenomenon and extreme variation was recorded for *Eutarsopolipus pungens* Husband and Dastych, 1998. This variation makes diagnostics based on males difficult. Similar variation in larvae and females has not been reported.

Constantine and Seeman (2014) described three new species of *Eutarsopolipus* that they placed in the *ochoai* species group. This decision was based on the original definition of the *ochoai* species group (Husband 1995) and the key to species groups in Husband and Husband (2009). Since Husband (1995), the *ochoai* species group has obtained nine members as defined by Constantine and Seeman (2014), but its definition has become less robust and overlaps with the *brettae* species group, as proposed by Husband (2002).

Species in the *ochoai* group may lack a respiratory system (*E. earnshawi*, *E. lambkinae*, *E. rutherfordae*; *E. scariteus* Husband, 2001; *E. weatherbyi* Husband and Psalmonds, 2004), show only the rudiments of stigmata (*E. ochoai* Husband, 1995), or have a well-developed respiratory system (*E. dastychi* Husband & Khaustov 2004; *E. leytei* Husband & Corpuz-Raros, 1995). Species of the *brettae* species group, which comprises only *E. brettae* Husband, 2002 and *E. obrieni* Husband and Husband, 2015, both lack a respiratory system. All these species retain claws on legs I–III, three setae on femur I, and at least one seta on genua I–III.

The presence/absence of a respiratory system is an important character in *Eutarsopolipus*. Several species

groups are defined by this feature, as shown in the key of Husband and Husband (2009), which has an error in its first couplet (the first couplet needs to be reversed). Therefore, it is unhelpful if this character is not used consistently to define species groups. For instance, *E. scariteus*—a member of the *ochoai* species group—will key to the *brettae* species group in Husband and Husband (2009). Furthermore, the rudimentary stigmata of *E. ochoa* need to be reassessed as they occur in an atypical position at the anterior margin of the prodorsal shield (and posteromesad the gnathosoma), so these may be another structure, as the stigmata are usually posterolaterad the gnathosoma in *Eutarsopolipus*.

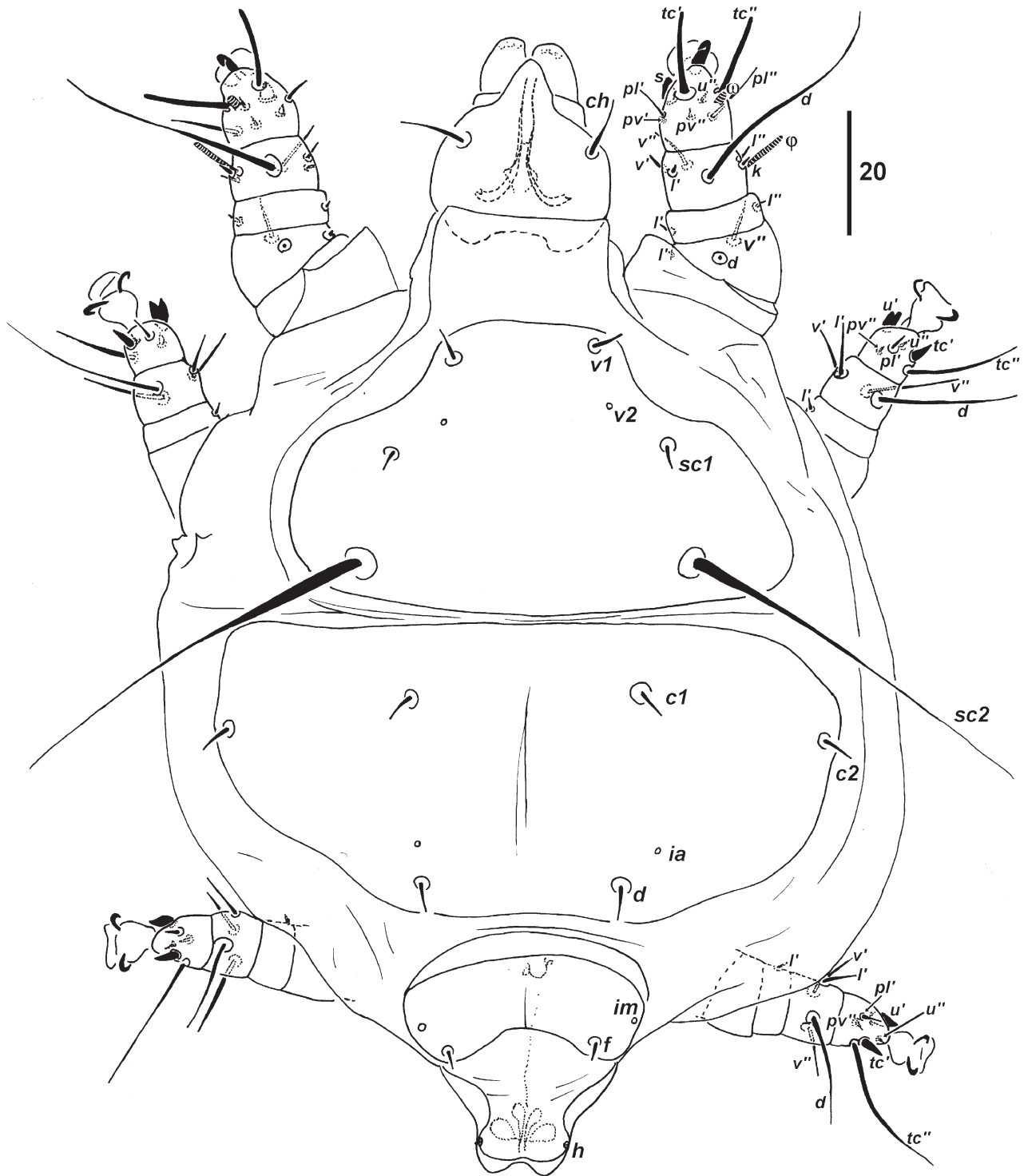


FIGURE 4. *Eutarsopolipus burwelli* sp. nov., larviform adult male, dorsum.

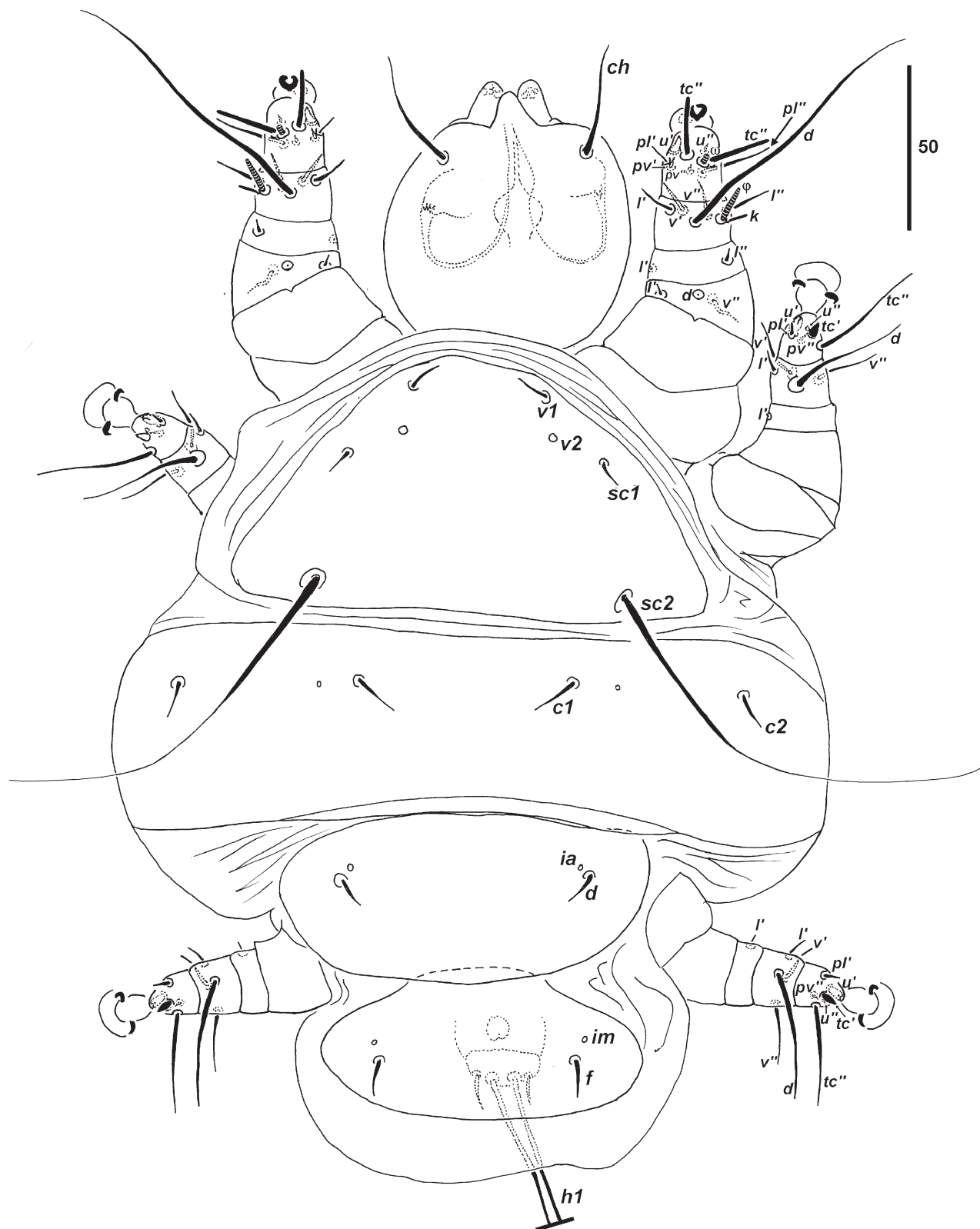


FIGURE 5. *Eutarsopolipus burwelli* sp. nov., larval female, dorsum.

A reformation of species groups based on phylogenetic analysis is needed, but in the interim it would seem best to define the *ochoai* species group in the manner originally intended, so that it includes only species with the respiratory system absent, retaining setae on all genua, and possessing claws on all legs. This definition includes the two



species from the *brettae* species group (*E. brettae*, *E. obrieni*) but excludes *E. dastychi* and *E. leytei*. The latter two species could be accommodated in the *leytei* species group, defined by the retention of a respiratory system, presence of claws on all legs, three femur I setae and presence of setae on all genua. Within the *ochoi* and *leytei* species groups, some reductions are apparent. Some species lack setae *l''* on genu I (*E. brettae*, *E. lambkinae*, *E. obrieni*) and males of some species have hypotrichous leg setation (*E. brettae*, *E. dastychi*, *E. lambkinae*, *E. ochoi*, *E. scariteus*). While the former character is homoplasious, the latter is found only in members of the *ochoi* and *leytei* species groups, and in the unusual species *Eutarsopolipus stammeri* Regenfuss, 1968, which has its own species group.

### *Eutarsopolipus echinatus* sp. nov.

**Diagnosis.** All life stages: respiratory system absent; tarsus II without solenidion; femur I with two setae (*v''* absent); genu I–III lacking setae; claws absent on legs I–III; setae *ch*, *v1*, *sc1*, *c1*, *c2*, *d*, *f* short, thorn-like. Adult female: gnathosomal length 44–46, width 43–46, cheliceral stylets long, 44–50; seta *h* absent; tarsi II–III with setae *u'* and *p'* in proximal position, seta *pv'* absent. Larviform adult male: setae *v1*, *sc1*, *c1*, *c2*, *f* short, length 2–3; leg setation same as female. Larval female: plates C and D separate; seta *h2* long, 33–44.

**Type material:** 4 females, 1 male, 5 larvae, all ex *Nurus medius*, as follows. **Australia: Queensland.** Holotype female, Eungella NP, Mt William, Site 1, 1234 masl, 21.016°S 148.598°E, 14 Nov. 2013, SC 25844, C. Burwell (QMS 110153, on same slide as paratype larva of *E. burwelli* QMS 110133). Paratypes: **1 female, 1 male, 1 larva**, same data as holotype (QMS 110154–56); **1 female**, Broken River, Eungella NP, 21° 10' 5"S 148°30'30"E, 17 Nov. 1992–15 Apr. 1993, IN7677, G. Monteith, D. Cook, HR# T82045 (ANIC 52-003933); **1 female**, Eungella NP, Dalrymple Heights, 21° 8'12"S 148°29'30"E, IN7864, 6 Jan. 1973, J. Hammond, HR# T82062 (QMS 110157); **1 female, 4 larvae**, Mt Macartney, 20°49'57"S 148°33'7"E, 19 Nov. 1992–15 Apr. 1993, IN5936, HR#T82035 (1 female, 1 larva ZMH-A0002399, ZMH-A0002400, 3 larvae QMS 110158–60); **1 larva**, Mt Macartney, same data except, HR# T82039 (ANIC 52-003934).

**Type deposition.** Holotype and most paratypes deposited in QM. One female, one larva deposited in ANIC, one female, one larva deposited in ZMH.

**Description. Female** (Figs 6–8, n = 4). *Gnathosoma*. Length 45 (44–46), width 46 (43–46). Palp length 14 (13–15). Cheliceral stylets 45 (44–50), pharynx width 13 (11–13), dorsal gnathosomal setae (*ch*) thorn-like, 2 (2–4), ventral setae (*su*) 7 (7–10), distance between ventral setae (*su–su*) 17 (17–19).

*Idiosoma*. Body not to slightly physogastric, ovate. Length 285 (215–305), width 210 (185–275). Respiratory system absent. Dorsal setae *v1*, *sc1*, *c1*, *c2*, *d*, *f* thorn-like. Prodorsal plate length 71 (65–75), with setae *v1* 6 (6–7), *v2* vestigial, *sc1* 7 (7–8), *sc2* 32 (31–35); *v2* anteromesad *sc1*. Distance between setae *v1–v1* 30 (28–35), *sc1–sc1* 79 (79–86), *v1–sc1* 37 (37–40), *v2–v2* 40 (39–44), *sc2–sc2* 89 (89–111), *sc1–sc2* 10 (10–12). Plates C, D, EF, H variously eroded medially, making widths variable. Plate C length 43 (38–43), setae *c1* 6 (5–6), setae *c2* 4 (4–5), distance between setae *c1–c1* 73 (73–94), *c1–c2* 54 (52–62). Plate D length 24 (24–40), setae *d* 4 (4–6), *d–d* 91 (84–93), cupuli *ia* anteromesad setae *d*. Plate EF length 30 (26–33), setae *f* 3 (2–3), *f–f* 66 (66–85); cupuli *im* anterolaterad setae *f*. Plate H length 11 (11–15), width 61 (55–62), setae *h* absent. Venter: small, thorn-like, *1a* minute (minute–1), *2a* 3 (2–3), *3a* 3 (2–3), *3b* 3 (2–3). Alveoli *1b*, *2b* apparent. Distance between setae *1a–1a* 29 (24–28), *2a–2a* 41 (30–41).

*Legs*. Setal counts legs I–III, femur-tarsus: 2-0-5(+ $\phi$ )-9(+ $\omega$ ), 0-0-4-7, 0-0-4-7. Leg I: femur I, *d* minute, *l'* 3 (2–3); tibia I, *d* 28 (25–28), *l'* 5 (4–5), *l''* 1 (1–2), *v'* 5 (4–5), *v''* 4 (4–5),  $\phi$  7 (7–9); tarsus I, *tc'* 10 (9–10), *tc''* 9 (9–10), *pl'* 7 (7–10), *pl''* 12 (10–12), *pv'* 3 (3–4), *pv''* 3 (3–4), *s* 6 (6–7),  $\omega$  2 (2), *p'* 1 (1), *u''* 2 (2–3). Leg II: tibia II, *d* 8 (8–10), *l'* 4 (4–5), *v'* 4 (4–5), *v''* 8 (8–12); tarsus II, *tc'* 5 (5), *tc''* 25 (23–26), *pl'* 17 (17–19), *pv''* 3 (3), *u'* 5 (5), *u''* 1 (1–2), *p'* 1 (1–2). Leg III: tibia III, *d* 7 (7–10), *l'* 4 (3–4), *v'* 4 (4–5), *v''* 7 (7–10); tarsus III, *tc'* 5 (5), *tc''* 32 (26–35), *pl'* 17 (17–21), *pv''* 2 (2–3), *u'* 5 (5), *u''* 1 (1–2), *p'* 3 (2–3). Tibia I seta *v'* spine-like; tarsus I setae *pv'*, *pv''* spine-like. Tibia II–III, seta *l'* spine-like; tarsi II–III setae *u'* spine-like, setae *p'*, *pv''* spine-like. Claws on legs I–III absent.

**Larviform adult male** (Fig. 7; n = 1). *Gnathosoma*. Length 33, width 35. Palp length 10. Cheliceral stylets 25, pharynx width 9, *ch* 2, *su* 5, *su–su* 14.



FIGURE 6. *Eutarsopolipus echinatus* sp. nov., adult female, dorsum.

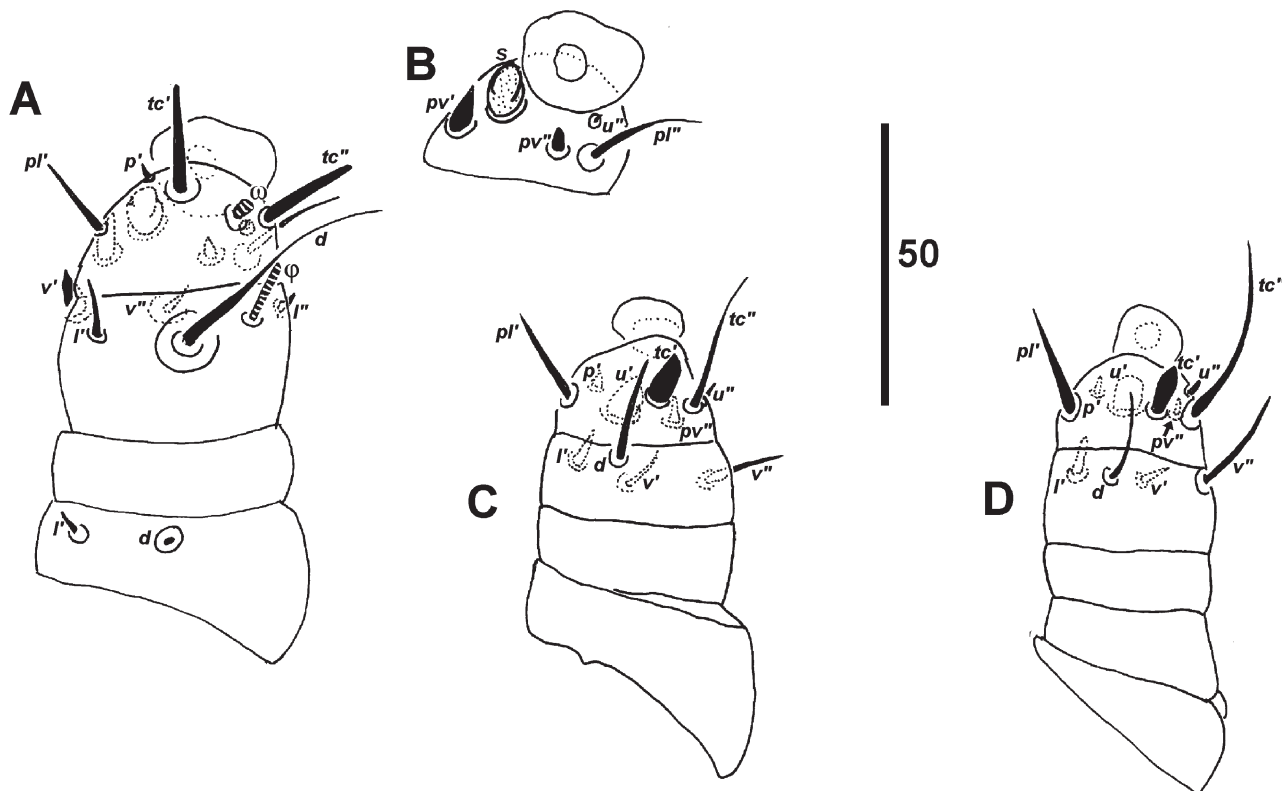


FIGURE 7. *Eutarsopolipus echinatus* sp. nov., adult female, venter.

*Idiosoma*. Length 180, width 155. Dorsal setae *vl*, *sc1*, *c1*, *c2*, *d*, *f* small, thickened to thorn-like. Prodorsal plate length 61, width 130, with setae *vl* 2, *v2* vestigial, *sc1* 2, *sc2* 16; *v2* anteromesad *sc1*. Distance between setae *vl*–*vl* 16, *sc1*–*sc1* 65, *vl*–*sc1* 28, *v2*–*v2* 23, *sc2*–*sc2* 69, *sc1*–*sc2* 12. Plate CD length 54, width 140, setae *c1* 3, *c2* 3, *d* 2; distance between setae *c1*–*c1* 52, *c1*–*c2* 36, *d*–*d* 39; cupuli *ia* antieriad setae *d*. Plate EF divided, each plate length 17, width 37, setae *f* 2, distance *f*–*f* 23; cupuli *im* anterolaterad setae *f*. Genital capsule length 23, width 37, setae *h* minute. Venter: coxal setae minute, alveoli *1b*, *2b* apparent. Distance between setae *1a*–*1a* 22, *2a*–*2a* 24.

*Legs*. Setal counts for legs I–III same as female; setal form similar. Leg I: femur I, *d* minute, *l'* 2; tibia I, *d* 25, *l'* 2, *l''* 2, *v'* 3, *v''* 5,  $\phi$  5, tarsus I, *tc'* 11, *tc''* 11, *pl'* 5, *pl''* 9, *pv'* 3, *pv''* 2, *s* 3, *p'* minute, *u''* 1,  $\omega$  2, left tarsus I with additional thorn-like seta between (*pv*). Leg II: tibia II, *d* 5, *l'* 4, *v'* 5, *v''* 9; tarsus II, *tc'* 5, *tc''* 16 (possibly broken), *pl'* 16, *pv''* 2, *u'* 4, *p'* 2, *u''* minute. Leg III: tibia III, *d* 4, *l'* 3, *v'* 5, *v''* 10; tarsus III, *tc'* 5, *tc''* 24, *pl'* 16, *pv''* 2, *u'* 5, *p'* 2, *u''* minute.

**Larval female** (Fig. 10; n = 5)



**FIGURE 8.** *Eutarsopolipus echinatus* sp. nov., adult female: (A) leg I, dorsal view; (B) tarsus I, ventral view; (C) leg II, dorsal view; (D) leg III, dorsal view.

*Gnathosoma*. Length 38–41, width 39–51. Palp length 11–14. Cheliceral stylets 41–46, pharynx width 10–12, *ch* 1–2, *su* 4–5, *su*–*su* 14–17.

*Idiosoma*. Length 175–215, width 135–240. Prodorsal plate length 64–69, width 115–135, with setae *vl* 4–5, *v2* vestigial, *sc1* 4–5, *sc2* 70–85; *v2* anteromesad *sc1*. Distance between setae *vl*–*vl* 23–26, *sc1*–*sc1* 60–69, *vl*–*sc1* 31–36, *v2*–*v2* 25–30, *sc2*–*sc2* 73–81, *sc1*–*sc2* 15–19. Plate C length 36–43, setae *c1* 4–5, setae *c2* 4–5. Plate D length 37–42, width 65–70, setae *d* 3–4, distance between setae *c1*–*c1* 51–56, *c1*–*c2* 49–57, *d*–*d* 37–41; cupuli *ia* antieriad setae *d*, distance *ia*–*d* 4–6. Plate EF length 32–40, width 55–65, setae *f* 2–3, distance *f*–*f* 38–41; cupuli *im* antieriad setae *f*, distance *im*–*f* 5–7. Plate H length 25–35, width 34–40, seta *h1* long, ca. 120, seta *h2* long, 33–44. Venter: coxal setae minute–1, distance between setae *1a*–*1a* 25–29, *2a*–*2a* 25–30.

*Legs*. Setal counts for legs I–III same as female; setal form similar. Leg I: femur I, *d* minute, *l'* 2; tibia I, *d* 40–47, *l'* 5–6, *l''* 2–3, *v'* 3, *v''* 8–10,  $\phi$  6–7; tarsus I, *tc'* 10–11, *tc''* 11–12, *pl'* 8–10, *pl''* 15–16, *pv'* 3, *pv''* 2, *s* 4–5, *p'* 2, *u''* 2,  $\omega$  3. Leg II: tibia II, *d* 7–9, *l'* 3–4, *v'* 6–8, *v''* 10–15; tarsus II, *tc'* 4–5, *tc''* 31–41, *pl'* 17–20, *pv''* 2, *p'* 3, *u'* 4, *u''* 2. Leg III: tibia III, *d* 7–8, *l'* 3–4, *v'* 6–7, *v''* 10–13; tarsus III, *tc'* 5, *tc''* 26–34, *pl'* 16–20, *pv''* 2–3, *p'* 3, *u'* 4–5, *u''* 2.



FIGURE 9. *Eutarsopolipus echinatus* sp. nov., larviform adult male, dorsum. “x” indicates asymmetrical seta on left tarsus I.

**Etymology.** The name *echinatus* (Latin: prickly, spiny; gender masculine) refers to the spine-like setae on the dorsum.

**Differential diagnosis.** The short, thorn-like setae are unlike any other species of *Eutarsopolipus*. This species fits the concept of the *pterostichi* species group, which is a heterogeneous collection of eight species that requires revision. Members of this group are generally regarded as species that lack both a respiratory system and setae on



genus II–III. However, it includes species with or without ambulacral claws and variable femur I and genu I setation, suggesting either homoplasious morphological reductions within this group or that it is polyphyletic. In lacking ambulacral claws on all legs and all genual setae, *E. echinatus* **sp. nov.** is similar to *E. inermis* Regenfuss, 1974 and *E. osunaharae* Husband and Kurosa, 2012, which are the only other species of the *pterostichi* group that share these character states. These species also share the loss of seta *v''* on femur I and seta *k* on tibia I. In addition to the absence of spine-like setae, *E. inermis* and *E. osunaharae* also differ in retaining a solenidion on tarsus II and having larvae with fused plates C and D.

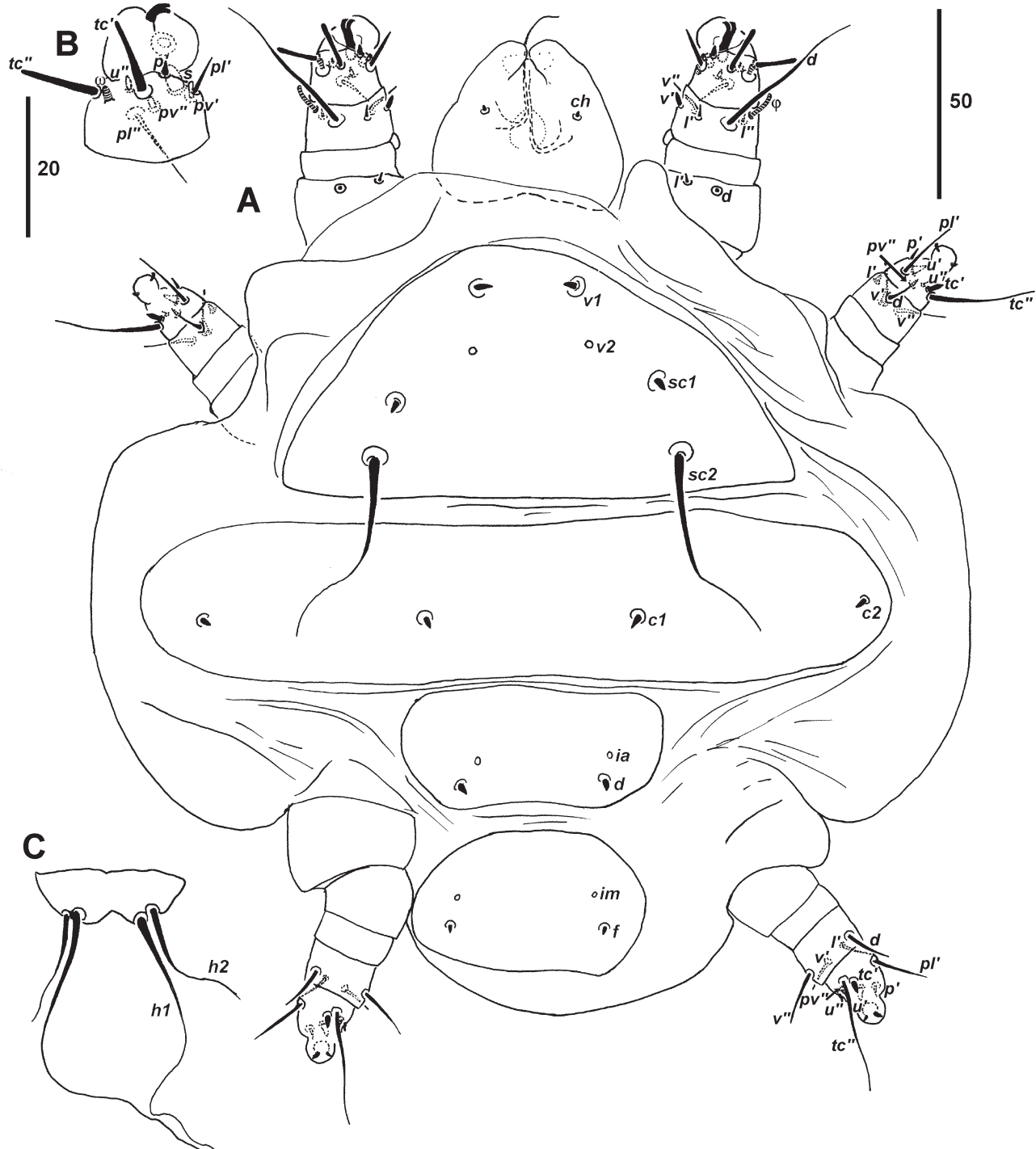


FIGURE 10. *Eutarsopolipus echinatus* **sp. nov.**, larval female: (A) dorsum; (B) tarsus I, detail; (C) Plate H (ventral).

**Remarks.** The species was found cohabiting with *E. burwelli* on the type host beetle and beetles T82062 and T82039.

The notations for the *p'* setae on tarsus II–III are tentative. Species of *Eutarsopolipus* may present a minute to small, distal seta on the anterior side of the tarsus. When this seta is proximal to the insertion of the spur-like seta *u''*, I have interpreted it as the retention of seta *pv'*, as in *E. earnshawi* (Constantine & Seeman 2013). When this seta is distal to the insertion of *u''*, I have designated the seta as *p'*. In *E. echinatus* **sp. nov.**, seta *u'* is in an unusual proximal position, so according to my interpretation, I have designated the small spine-like anteroventral seta as *p'*, which is assumed to have migrated ventrally with *u'*.

## Key to species groups of *Eutarsopolipus* (Adult females)

The following key aims to reduce the number of species groups by eliminating graded characters (size of claws, length of setae and cheliceral stylets) as group-defining features. The groups removed from the key of Husband and Husband (2009) each comprised just 1–2 species.

1.	Respiratory system (stigmata and tracheae) absent	2
-	Respiratory system (stigmata and tracheae) present	4
2.	Genu II–III setae absent	<i>pterostichi</i> <sup>1</sup>
-	Genu II–III setae present	3
3.	Ambulacral claws I–III prominent, with idiosomal plates	<i>ochoi</i> <sup>2</sup>
-	Ambulacral claws I–III absent, without idiosomal plates	<i>stammeri</i>
4.	Ambulacral claws II–III absent	5
-	Ambulacral claws II–III present	6
5.	Ambulacral claws I absent	<i>biunguis</i>
-	Ambulacral claws I present	<i>acanthomus</i>
6.	Genu II–III setae present	<i>leytei</i> <sup>3</sup>
-	Genu II–III setae absent	7
7.	Two genu I setae	8
-	No genu I setae	9
8.	Three femur I setae ( <i>v''</i> present)	<i>megacheli</i>
-	Two femur I setae ( <i>v''</i> absent)	<i>secundus</i>
9.	Tarsus II solenidion present	<i>myzus</i> <sup>4</sup>
-	Tarsus II solenidion absent	<i>lagenaeformis</i>

<sup>1</sup> The *pterostichi* species group is combined with the *lukoschusi* species group. The latter includes just one species defined by its smaller claws, which is not considered a strong character for delimiting species groups, especially considering that two members of the *pterostichi* species group have claws that are small or absent (*E. inermis*, *E. osunaharae*).

<sup>2</sup> Includes the *brettae* species group. See *Remarks* for *E. burwelli*.

<sup>3</sup> The *leytei* species group here comprises *E. dastychi* and *E. leytei*. See *Remarks* for *E. burwelli*.

<sup>4</sup> The *myzus* group incorporates the *crassiceps* and *desani* groups as their defining features seem minor (size of claws for the *crassiceps* group, intermediate length of *h1* for the *desani* group) and they fit well into the concept of the *myzus* group.

## Discussion

Synhospitality—the association of two or more closely related species on the same host species—is often recorded for parasitic species, such as ticks (e.g., Chilton *et al.* 1992), mites (e.g., Bochkov & Saveljev 2012), plasmodiids (e.g., Pérez-Tris *et al.* 2007), Monogenea (e.g., Simková *et al.* 2000) and Cestoda (e.g., Friggens & Brown 2005). The parasite species need not be closest relatives. Rather, observation and discussion of synhospitally parasites usually involves species classified in the same genus. In this sense, synhospitality is common in Podapolipidae (e.g., Husband *et al.* 2008; Seeman & Nahrung 2005, 2013; Seeman 2008; Hajiqaanbar & Joharchi 2011; Katlav *et al.* 2014). In *Eutarsopolipus*, two species is typical (*n* = 14 beetle species), but *Poecilus cupreus* (L.), *Stenolophus lacordairei* (Chaudoir) and possibly *Agonum sexpunctatum* (L.) have three (Table 1).

The term synhospitality is little-used. Originally coined by Eichler (1966), its purpose was to distinguish between parasites that show geographic sympatry but live on different hosts, and those that share the same host species. Regenfuss (1968, 1972) used the term for Podapolipidae, and it has continued to be used for this group of mites

(e.g., Husband *et al.* 2008; Katlav *et al.* 2014). A few other acarologists have employed the term (e.g., Desch & Nutting 1972; Bochkov & Mironov 2008), as have some other parasitologists (e.g., Holmes 1973; Shuttleworth *et al.* 2016) and, more interestingly, it has been used by entomologists for drosophilid flies that breed in inflorescences (e.g., Yafuso 2008). Other parasitologists tend to discuss the presence of parasites on a host in terms of niche segregation (e.g., Šimková *et al.* 2002), although such concepts do not strictly require parasitic species in the same genus (e.g., Fernández-González *et al.* 2015).

**TABLE 1.** Species of *Eutarsopolipus* (Podapolipidae) found on the same host species.

Host species	Mite species	Species group	Reference
Beetles with mites in the same species groups			
<i>Agonum sexpunctatum</i>	<i>E. agonobius</i>	<i>biunguis</i>	Regenfuss (1968)
	<i>E. brevici</i> *	<i>biunguis</i>	Husband and Dastych (2002)
	<i>E. sphaericus</i> **		Regenfuss (1972)
<i>Amara aenea</i>	<i>E. amaraceus</i>	<i>acanthomus</i>	Tajodin <i>et al.</i> (2014)
	<i>E. elongatus</i>	<i>acanthomus</i>	Regenfuss (1968)
<i>Amara similata</i>	<i>E. assimilis</i>	<i>acanthomus</i>	Eidelberg (1994)
	<i>E. crassisetus</i>	<i>acanthomus</i>	Eidelberg (1994)
<i>Broscus cephalotes</i>	<i>E. alarum</i>	<i>acanthomus</i>	Regenfuss (1968)
	<i>E. acanthomus</i>	<i>acanthomus</i>	Regenfuss (1968)
<i>Broscus semistriatus</i>	<i>E. alarum</i>	<i>acanthomus</i>	Regenfuss (1968)
	<i>E. assimilis</i>	<i>acanthomus</i>	Regenfuss (1968)
			Regenfuss (1968)
<i>Chlaenius prasinus</i>	<i>E. americanus</i>	<i>myzus</i>	Husband and Husband (2013)
	<i>E. hemistylus</i>	<i>myzus</i>	Husband and Husband (2014)
<i>Chlaenius sericeus</i>	<i>E. davidsoni</i>	<i>myzus</i>	Husband (2000)
	<i>E. pungens</i>	<i>myzus</i>	Husband and Dastych (1998)
<i>Poecilus cupreus</i>	<i>E. abdominis</i>	<i>myzus</i>	Regenfuss (1968)
	<i>E. squamarum</i>	<i>myzus</i>	Regenfuss (1968)
	<i>E. thoracis</i>	<i>myzus</i>	Regenfuss (1968)
			Regenfuss (1968)
<i>Poecilus lepidus</i>	<i>E. myzus</i>	<i>myzus</i>	Regenfuss (1968)
	<i>E. poecili</i>	<i>myzus</i>	Regenfuss (1968)
<i>Stenolophus comma</i>	<i>E. brevichelus</i>	<i>biunguis</i>	Husband and Husband (2003)
	<i>E. elzingai</i>	<i>biunguis</i>	Husband (1998)
<i>Stenolophus lecontei</i>	<i>E. brevichelus</i>	<i>biunguis</i>	Husband and Husband (2003)
	<i>E. elzingai</i>	<i>biunguis</i>	Husband (1999)
	<i>E. porter</i>	<i>acanthomus</i>	Husband (1993)
<i>Syntomus lateralis</i>	<i>E. gombrooni</i>	<i>myzus</i>	Hajiqanbar <i>et al.</i> (in press)
	<i>E. oconnori</i>	<i>myzus</i>	Hajiqanbar <i>et al.</i> (in press)
Beetles with mites in different species groups			
<i>Catadromus lacordairei</i>	<i>E. megacheli</i>	<i>megacheli</i>	Husband and Macfarlane (1999)
	<i>E. secundus</i>	<i>secundus</i>	Husband and Macfarlane (1999)
<i>Chlaenius aestivus</i>	<i>E. inermis</i>	<i>pterostichi</i>	Regenfuss (1974)
	<i>E. latus</i>	<i>myzus</i>	Regenfuss (1974)
<i>Pterostichus melanarius</i> ***	<i>E. pterostichi</i>	<i>pterostichi</i>	Regenfuss (1968)
	<i>E. stammeri</i>	<i>stammeri</i>	Regenfuss (1968)
<i>Nurus medius</i>	<i>E. burwelli</i> <b>sp. nov.</b>	<i>ochoai</i>	this paper
	<i>E. echinatus</i> <b>sp. nov.</b>	<i>pterostichi</i>	this paper

\* = *E. oblongus* in Regenfuss (1972); \*\* = a nomen nudum; \*\*\* = as *P. vulgaris* in Regenfuss (1968)

Bochkov and Mironov (2008) distinguished two main types of synhospitality. The first involves species that are not closest relatives and at least one must therefore have switched host species. The second involves species that are closest relatives, which they term phylogenetic synhospitality. Two mechanisms can lead to phylogenetic synhospitality. The first occurs by allopatry, where isolated host populations have resulted in parasite speciation but not host speciation. The other pathway involves sympatric (synxenic) speciation, where mites speciate by specialisation to specific microhabitats on one host species. In the first case, we might expect the species to be morphologically similar because they still occupy the same species and same microhabitat—so much so that they may be morphologically cryptic. Host populations may also be allopatric. In the second case, the species must occupy different microhabitats, and their morphology often reflects adaptations to this habitat.

In *Eutarsopolipus*, most cases of synhospitality involve mites in the same species group ( $n = 12$ ), so these could be very closely related and cases of phylogenetic synhospitality. Without a phylogeny, we cannot be sure, but Regenfuss (1972) demonstrated that different species of *Eutarsopolipus* occupy at least seven different microhabitats beneath the elytra of their host—eight, if his footnote recording *E. stammeri* as an endoparasite is included. These seven microhabitats occur on the dorsal abdomen and the fore and hind wings. For instance, *E. brevic* Husband and Dastych, 2002 (as *E. oblongus* in Regenfuss (1972), a nomen nudum) lives on the proximal portion of the hindwing, while *E. agonobius* utilises the anterolateral underside of the forewing. Regenfuss (1972) thought that *E. brevic* and *E. agonobius* were unrelated (thus indicating a host-switching model), but Husband and Dastych (2002) and Mortazavi *et al.* (2014) consider these two species closely related to each other.

In the other four cases of synhospitality, including *E. burwelli* **sp. nov.** and *E. echinatus* **sp. nov.**, the species belong to different species groups (Table 1). This represents host-switching, and—when the same pairs of species groups are found on related hosts—-independent species radiations that may involve co-speciation with their hosts. Such a model was hypothesised for the Australian *Chrysomelobia*. In this case, three mite species from three separate species groups are found on different species of *Paropsis* (Seeman 2008; Seeman & Nahrung 2013). While one group (the *lawsoni* group) infests the tracheae of their hosts, no specific microhabitat preferences were noted for members of the other two groups (the *giml* and *husbandi* groups). A similar radiation may exist for *Eutarsopolipus* on Australian pterostichine carabid beetles. Preliminary surveys for Podapolipidae on Pterostichinae have revealed other members of the *ochoi* and *pterostichi* species groups in synhospitality, suggesting a diverse fauna of *Eutarsopolipus* remains to be described on these beetles.

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## References

- Berlese, A. (1911) Acarorum species novae quindecim. *Redia*, 7, 429–435.
- Berlese, A. (1913) Acari Nuovi. *Redia*, 9, 27–87.  
[https://doi.org/10.1016/S0033-3506\(13\)80183-7](https://doi.org/10.1016/S0033-3506(13)80183-7)
- Bochkov, A.V. & Mironov, S.V. (2008) The phenomenon of phylogenetic synhospitality in acariform mites (Acari: Acari-formes)—the permanent parasites of vertebrates. *Parazitologiya*, 42, 81–100.
- Bochkov, A.V. & Saveljev, A.P. (2012) Fur mites of the genus *Schizocarpus* Trouessart (Acari: Chirodiscidae) from the Eurasian beaver *Castor fiber tuvinicus* Lavrov (Rodentia: Castoridae) in the Azas River (Tuva Republic, Russia). *Zootaxa*, 3410 (1), 1–18.  
<https://doi.org/10.11646/zootaxa.3410.1.1>
- Chilton, N.B., Bull, C.M. & Andrews, R.H. (1992) Niche segregation in reptile ticks: attachment sites and reproductive success of females. *Oecologia*, 90, 255–259.  
<https://doi.org/10.1007/BF00317183>

- Constantine, R.A. & Seeman, O.D. (2014) Three new species of *Eutarsopolipus* (Acari: Podapolipidae) from Australian carabid beetles (Coleoptera: Carabidae). *Systematic & Applied Acarology*, 19, 87–109.  
<https://doi.org/10.11158/saa.19.1.8>
- Desch, C. & Nutting, W.B. (1972) *Demodex folliculorum* (Simon) and *D. brevis* Akbulatova of Man: redescription and reevaluation. *The Journal of Parasitology*, 58, 169–177.  
<https://doi.org/10.2307/3278267>
- Eichler, W. (1966) Two new evolutionary terms for speciation in parasitic animals. *Systematic Zoology*, 15, 216–218.  
<https://doi.org/10.2307/2411393>
- Eidberg, M.M. (1994) Mites of the family Podapolipidae (Heterostigmata, Tarsonemina) of Ukraine and adjacent areas with description of a new species. *Vestnik Zoologii*, 1994, 37–43.
- Ewing, H.E. (1922) Studies on the taxonomy and biology of tarsonemid mites, together with a note on the transformation of *Acarapis* (*Tarsonemus*) *woodi* Renn (Acarina). *Canadian Entomologist*, 54, 104–113.  
<https://doi.org/10.4039/Ent54104-5>
- Fernández-González, S., Pérez-Rodríguez, A., de la Hera, I., Proctor, H.C. & Pérez-Tris, J. (2015) Different space preferences and within-host competition promote niche partitioning between symbiotic feather mite species. *International Journal for Parasitology*, 45, 655–662.  
<https://doi.org/10.1016/j.ijpara.2015.04.003>
- Friggens, M.M. & Brown, J.H. (2005) Niche partitioning in the cestode communities of two elasmobranchs. *Oikos*, 108, 76–84.  
<https://doi.org/10.1111/j.0030-1299.2005.13275.x>
- Hajiyanbar, H. & Joharchi, O. (2011) World distribution and host range of *Podapolipoides* spp. (Acari: Heterostigmata: Podapolipidae), with the description of a new species. *Systematic Parasitology*, 78, 151–162.  
<https://doi.org/10.1007/s11230-010-9284-5>
- Hajiyanbar, H. & Mortazavi, A. (2012) First record of the *myzus* species group (Acari: Podapolipidae: *Eutarsopolipus* Berlese, 1911) from Asia, with the description of two new species parasitising carabid beetles. *Systematic Parasitology*, 83, 189–202.  
<https://doi.org/10.1007/s11230-012-9384-5>
- Hajiyanbar, H., Mortazavi, A. & Khaustov, A. (2019) Two new species of *Eutarsopolipus* (Acari: Prostigmata: Podapolipidae) parasitising carabid beetles from Iran. *Zootaxa*, 4647 (1), 154–167.  
<https://doi.org/10.11646/zootaxa.4647.1.13>
- Holmes, J.C. (1973) Site selection by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities. *Canadian Journal of Zoology*, 51, 333–347.  
<https://doi.org/10.1139/z73-047>
- Hurst, G.D.D., Sharpe, R.G., Broomfield, A.H., Walker, L.E., Majerus, T.M.O., Zakharov, I.A. & Majerus, M.E.N. (1995) Sexually transmitted disease in a promiscuous insect, *Adalia bipunctata*. *Ecological Entomology*, 20, 230–236.  
<https://doi.org/10.1111/j.1365-2311.1995.tb00452.x>
- Husband, R.W. (1993) A new *Eutarsopolipus* (Acari: Podapolipidae); parasite of *Harpalus herbivagus* (Coleoptera: Carabidae) from Michigan. *The Great Lakes Entomologist*, 26, 1–14.
- Husband, R.W. (1995) A new species of *Eutarsopolipus* (Acari: Podapolipidae) from Costa Rican *Pasimachus* spp. (Coleoptera: Carabidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 11, 157–165.
- Husband R.W. (1998) New species of *Eutarsopolipus* (Acari: Podapolipidae) from *Harpalus caliginosus* (F.) and *Agonodorus comma* (F.) (Coleoptera: Carabidae) from Kansas and Wyoming, U.S.A. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 12, 255–264.
- Husband, R.W. (1999) American *Eutarsopolipus* of the *biunguis* group and descriptions of previously unknown male and larval female of *Eutarsopolipus trichognathi* (Acari: Podapolipidae) from South America. *International Journal of Acarology*, 25, 13–17.  
<https://doi.org/10.1080/01647959908683606>
- Husband, R.W. (2000) *Eutarsopolipus davidsoni* n. sp. (Acari: Podapolipidae) from *Chlaenius sericeus* (Coleoptera: Carabidae) from Ingham County, Michigan, and redescription of male *Eutarsopolipus regenfussi*. *The Great Lakes Entomologist*, 33, 107–116.
- Husband, R.W. (2001) A new species of *Eutarsopolipus* (Acari: Podapolipidae) from *Scarites subterraneus* (Coleoptera: Carabidae) from Louisiana, U.S.A. *International Journal of Acarology*, 27, 113–117.  
<https://doi.org/10.1080/01647950108684238>
- Husband, R.W. (2002) A new species of *Eutarsopolipus* Berlese (Acari: Podapolipidae) from the Galapagos Islands, a parasite of *Agonum chathamii* Van Dyke (Coleoptera: Carabidae). *Proceedings of the Entomological Society of Washington*, 104, 563–570.
- Husband, R.W. & Corpuz-Raros, L.A. (1989) A new species of *Podapolipus* and a new species of *Eutarsopolipus* (Acari: Podapolipidae) from the Philippines. *Philippine Entomologist*, 7, 525–536.
- Husband, R.W. & Dastych, H. (1998) A new species of *Eutarsopolipus* (Acari: Podapolipidae) from *Chlaenius sericeus* Frost (Coleoptera: Carabidae) from Athens, Georgia, U.S.A. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 12, 317–326.



- Husband, R.W. & Dastych, H. (2002) A new species of *Eutarsopolipus* Berlese (Acari: Podapolipidae) from *Agonum sexpunctatum* (L.) (Coleoptera: Carabidae) from Germany and notes on the *biunguis*-group of *Eutarsopolipus*. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 14, 39–51.
- Husband, R.W. & Husband, D.O. (2003) New records of *Crotalomorpha camini* Lindquist and Krantz (Acari: Crotalomorphidae) and a new species of *Eutarsopolipus* (Acari: Podapolipidae) parasitic on *Stenolophus (Agonodorus) lecontei* (Chaudoir) (Coleoptera: Carabidae) from the central United States. *International Journal of Acarology*, 29, 339–344.  
<https://doi.org/10.1080/01647950308684350>
- Husband, R.W. & Husband, D.O. (2009) A review of the *pterostichi* group of *Eutarsopolipus* and a description of a new species of *Eutarsopolipus* (Acari: Podapolipidae), parasite of *Platynus teter* (Coleoptera: Carabidae) in Chiapas, Mexico. *Annals of the Entomological Society of America*, 102, 1062–1067.  
<https://doi.org/10.1603/008.102.0614>
- Husband, R.W. & Husband, D.O. (2013) *Eutarsopolipus americanus* sp. nov. (Acari: Podapolipidae), subelytral parasite of *Chlaenius praesinus* Dejean (Coleoptera: Carabidae) from Michigan and Missouri, USA. *Systematic & Applied Acarology*, 18, 53–60.  
<https://doi.org/10.11158/saa.18.1.6>
- Husband, R.W. & Husband, D.O. (2014) *Eutarsopolipus hemistylus* sp. nov. (Acari: Podapolipidae), subelytral parasite of *Chlaenius prasinus* Dejean (Coleoptera: Carabidae) from central and eastern USA. *The Great Lakes Entomologist*, 47, 25–31.
- Husband, R.W. & Husband, D.O. (2015) *Eutarsopolipus obrieni* n. sp. (Acari: Podapolipidae), ectoparasite of *Platynus darlingtoni* (Coleoptera: Carabidae) in Jamaica, a second species in the *brettae* group of *Eutarsopolipus*. *Systematic & Applied Acarology*, 20, 967–976.  
<https://doi.org/10.11158/saa.20.8.12>
- Husband, R.W. & Khaustov, A. (2004) A new species of *Eutarsopolipus* (Acari: Podapolipidae) from *Calathus fuscipes* (Coleoptera: Carabidae) from Ukraine. *International Journal of Acarology*, 30, 329–333.  
<https://doi.org/10.1080/01647950408684401>
- Husband, R.W. & Kurosa, K. (2012) *Eutarsopolipus osunaharae* sp. nov. (Acari: Podapolipidae), subelytral parasite of *Diplocheila zeelandica* (Redtenbacher) (Coleoptera: Carabidae) from Japan. *Systematic & Applied Acarology*, 17, 83–90.  
<https://doi.org/10.11158/saa.17.1.14>
- Husband, R.W. & Macfarlane, D. (1999) Two new species of *Eutarsopolipus* (Acari: Podapolipidae) from *Catadromus lacordairei* (Coleoptera: Carabidae) from Australia. *International Journal of Acarology*, 25, 297–308.  
<https://doi.org/10.1080/01647959908684168>
- Husband, R.W. & Psalmonds, L. (2004) A new species of *Eutarsopolipus* (Acari: Podapolipidae) from *Scarites* sp. (Coleoptera: Carabidae) from Argentina. *International Journal of Acarology*, 30, 107–112.  
<https://doi.org/10.1080/01647950408684377>
- Husband, R.W., Husband, P.S. & Husband, D.O. (2008) Observations on synhospitality including records of three genera of Podapolipidae (Acari: Tarsonemina) parasitic on *Schistocerca nitens* (Thunberg) (Orthoptera: Acrididae) from California, U.S.A. *International Journal of Acarology*, 34, 71–83.  
<https://doi.org/10.1080/01647950808683707>
- Katlav, A. & Hajiqanbar, H. (2018) First description of male and larval female of parasitic mite *Eutarsopolipus abdominis* (Acari: Podapolipidae) with redescription of the adult female. *Journal of Parasitology*, 104, 1–9.  
<https://doi.org/10.1645/17-152>
- Katlav, A., Hajiqanbar, H. & Talebi, A.A. (2014) *Dorsipes caspius* n. sp. (Acari: Podapolipidae), a subelytral parasite of *Pterostichus caspius* (Menetries) (Coleoptera: Carabidae) with notes on host range of the genus and the distribution of the *platysmae* group. *Systematic Parasitology*, 89, 117–132.  
<https://doi.org/10.1007/s11230-014-9512-5>
- Lindquist, E.E. (1986) The world genera of Tarsonemidae (Acari: Heterostigmata): A morphological, phylogenetic, and systematic revision, with a reclassification of family group taxa in Heterostigmata. *Memoirs of the Entomological Society of Canada*, 136, 1–517.  
<https://doi.org/10.4039/entm118136fv>
- Mortazavi, A., Hajiqanbar, H. & Kamali, K. (2014) First record of the *biunguis* species group (Acari: Podapolipidae: *Eutarsopolipus*) from Asia, with the description of a new species parasitizing *Drypta lineola* (Coleoptera: Carabidae). *Annals of the Entomological Society of America*, 107, 449–556.  
<https://doi.org/10.1603/AN13196>
- Pérez-Tris, J., Hellgren, O., Križanauskienė, A., Waldenström, J., Secondi, J., Bonneaud, C., Fjeldså, J., Hasselquist, D. & Bensch, S. (2007) Within-Host Speciation of Malaria Parasites. *PLoS ONE*, 2 (2), e235.  
<https://doi.org/10.1371/journal.pone.0000235>
- Regenfuss, H. (1968) Untersuchungen zur Morphologie, Systematic und Ökologie der Podapolipidae (Acarina: Tarsonemini). *Zeitschrift für Wissenschaftliche Zoologie*, 177, 183–282.
- Regenfuss, H. (1972) Über die Einnischung synhospitaler Parasitenarten auf dem Wirtskörper: Untersuchungen an ektoparasitischen Milben (Podapolipidae) auf Laufkäfern (Carabidae). *Sonderdruck aus Zeitschrift für zoologische Systematik und Evolutionsforschung*, 10, 44–65.

- <https://doi.org/10.1111/j.1439-0469.1972.tb00784.x>
- Regenfuss, H. (1974) Neue ektoparasitische Arten der familie Podapolipidae (Acari: Tarsonemina) von Carabiden. *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut*, 71, 147–163.
- Seeman, O.D. (2008) Systematics and phylogeny of *Chrysomelobia* species (Acari: Podapolipidae), sexually transmitted parasites of chrysomelid beetles. *Invertebrate Systematics*, 22, 55–84.  
<https://doi.org/10.1071/IS06035>
- Seeman, O.D. & Nahrung, H.F. (2004) Female biased parasitism and the importance of host generation overlap in a sexually-transmitted parasite of beetles. *Journal of Parasitology*, 90, 114–118.  
<https://doi.org/10.1645/GE-101R1>
- Seeman, O.D. & Nahrung, H.F. (2005) New *Parobia* (Acari: Podapolipidae) parasitic on pestiferous paropsine beetles (Coleoptera: Chrysomelidae) in eucalypt plantations. *Systematic & Applied Acarology*, 10, 111–135.  
<https://doi.org/10.11158/saa.10.1.12>
- Seeman, O.D. & Nahrung, H.F. (2013) Two new species of *Chrysomelobia* Regenfuss, 1968 (Acariformes: Podapolipidae) from *Paropsis charybdis* Stål (Coleoptera: Chrysomelidae). *Systematic Parasitology*, 86, 257–270.  
<https://doi.org/10.1007/s11230-013-9447-2>
- Shuttleworth, M.A., Jabbar, A. & Beveridge, I. (2016) Description and molecular characterisation of *Cloacina johnstoni* sp. nov. (Nematoda: Strongyloidea) from the wallaroo, *Macropus robustus* (Marsupialia: Macropodidae) and relationships with the synhospitalic species *C. macropodis*. *Parasitology Research*, 116, 3357–3363.  
<https://doi.org/10.1007/s00436-016-5096-0>
- Šimková, A., Desdevises, Y., Gelnar, M. & Morand, S. (2000) Co-existence of nine gill ectoparasites (Dactylogyrus: Monogenea) parasitising the roach (*Rutilus rutilus* L.): history and present ecology. *International Journal for Parasitology*, 30, 1077–1088.  
[https://doi.org/10.1016/S0020-7519\(00\)00098-9](https://doi.org/10.1016/S0020-7519(00)00098-9)
- Šimková, A., Ondračková, M., Gelnar, M. & Morand, S. (2002) Morphology and coexistence of congeneric ectoparasite species: reinforcement of reproductive isolation. *Biological Journal of the Linnean Society*, 76, 125–135.  
<https://doi.org/10.1111/j.1095-8312.2002.tb01719.x>
- Tajodin, M., Hajiqaanbar, H. & Talebi, A.A. (2014) A new species description of the *acanthomus* species group (Acari: Podapolipidae: *Eutarsopolipus*), with keys to world species of the group. *Applied Entomology and Zoology*, 49, 109–117.  
<https://doi.org/10.1007/s13355-013-0230-2>
- Yafuso, M. (2008) Life history traits related to resource partitioning between synhospitalic species of *Colocasiomyia* (Diptera, Drosophilidae) breeding in inflorescences of *Alocasia odora* (Araceae). *Ecological Entomology*, 19, 65–73.  
<https://doi.org/10.1111/j.1365-2311.1994.tb00391.x>